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ONTOGENETIC MORPHOGENESIS AND ENVIRONMENT

- USSR -

by G. A. Shmidt

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In discussing various questions concerning the theory of individual development, one must take into account the specific characteristics of ontogenetic morphogenesis. First of all, one must bear in mind the complexity of the internal mechanisms of the individual development of animals. This is explainable by the complex interrelation of the living organism with its environment. On the other hand, it reflects the necessity, in a relatively short time, to effect this development from the cellular embryo to the sexually-mature state.

Adaptive Changes—The Source of the Evolution of Ontogenesis

The primary importance of the adaptive processes in the changes of ontogenesis is discovered comparatively more easily in cases when the developing organism possesses in the embryonic or larval stage clearly-defined adaptive signs. As an example, one can cite the bony fishes which have clearly-delineated adaptive signs from the moment when the egg is dropped, to its insemination and the further process of the formation of the larva and its free existence after it comes out of the egg.

The initial type of biology of reproduction for all multicellular organisms is connected with free larval development (G. A. Shmidt, 1951, Chap. 9). It is characterized by the laying of small-sized eggs into the water, prior to insemination, usually one at a time.

From the stage of free larval development, there has been formed, through the process of evolution, in various groups (coelenterata, ciliated worms, Nemertini, Annelida, roundworms, mollusks, Arthropoda, and Chordata) a non-larval type of embryogenesis. Usually, in the biology of reproduction, this type of development corresponds to egg-laying and internal insemination. The embryo develops under the protection of the egg-membranes up to the formation of the young form, having a supply of food in the plasma of the egg (and then in the plasma of the embryonic cells or in the yolk sac). In non-larval development, the participation of the maternal animal is far more distinctly evident both in the biology of reproduction and in the type of embryogenesis than in cases of free larval development. It can be expressed, first of all, in the following:

1. The nutrition of the embryo by food (the yolk) which, in the ovary, is deposited in the plasma of the egg in the process of ovogenesis during the period of the greatest growth of the ovocyte of the first order.

2. The formation, within the organism of the maternal animal, of egg membranes protecting the embryo from drying out or other unfavorable effects of the environment.

Adaptations pertaining to the nourishment of the embryo and the egg membranes have been defined by B. S. Matveyev (1939) as ovo adaptations. They can be defined also as adaptations which are formed in the organism of the maternal animal (G. A. Shmidt, 1946).

The study of these adaptations within the limits of a single species does not give a conception of their origin or of their subsequent changes. These data can be obtained only when one compares the development of allied species, which sharply differ in their type of development and, correspondingly, in their ecology. Thus, one can compare the initial species, having a free larval development, with the derivative, having a non-larval development. From a non-larval development there originates, in various groups, a secondary larval development in which, in their turn, sub-types can be distinguished: the encapsulated larval sub-type in the embryogenesis of Annelida, mollusks, flatworms, and others; (2) larval development in live birth (the primary-tracheal, marsupial and placental mammals and certain others (see G. A. Shmidt, 1951).

If closely-related species are compared to each other, when these species possess clear cut differences in relation to their ecology and in their types of development, both in the biology of reproduction and in embryogenesis, then data can be obtained concerning the influence of changes in maternal adaptations for defense against unfavorable influences of the environment upon the embryogenesis of the daughter organism.

We shall examine such an instance of the interrelation of two species in which the initial species has a non-larval development and the derivative, an encapsulated larval one. The author succeeded in finding such material in two successively connected species of littoral Nemertini.

The initial species, which has a non-larval development, inhabits the lower horizons of the littoral and the derivative the higher horizons (G. A. Shmidt, 1946 and 1956; G. A. Shmidt and M. N. Ragozina, 1955). The two species differ not only in their adaptations to the safeguarding of the daughter organisms in their development, depending on the maternal organism, but in many peculiarities of embryogenesis. In this case, the successively-connected forms have sharply distinct types of structures of their egg-membranes, have different quantitatives of nutritive egg-yolk and many differences in the ecology of the mature forms and the processes of embryogenesis.

The initial species, the littoral Nemertina Lineus desori, a non-larval type, with the entire development of the embryo and the formation of the Nemertina proceeding at the expense of the supply of egg yolk in the egg plasma, obtained in the gonad of the maternal animal. The egg membranes are formed from the excretions of skin glands. The sausage-like egg cord of this Nemertina contains a liquid basic substance, which contains numerous groups of eggs, disposed in separate, rather small capsules, formed in the gonad. These secondary egg capsules are called egg bubbles or tubes. The egg cord is covered by tender membranes. The eggs of this Nemertina are rather large (the diameter of the egg is about 350 u).

The Nemertina Lineus desori inhabits the lower horizons of the shore and here, during the reproductive season, it deposits its egg tubes. Insufficiently protected by the egg membranes during outgoing tides, the embryos of Lineus desori have an additional adaptation in the form of a third, provisional ectoderm.

From the species Lineus desori there arose a new species, Lineus ruber, which transferred its habitation to the higher horizons of the shore, where the egg deposits of this Nemertina remain for longer periods outside of the water. Corresponding with the new conditions of existence, the thin membranes of the egg-deposit were replaced by heavy membranes, and the basic substance of the deposit became denser. Upon the basis of these new, maternal adaptations, that is, on the basis of the adaptive changes in the maternal organism, which ensures a better defense of the embryo against drying out, certain signs of embryogenesis

have changed: the provisional ectoderm, which, in the initial species was non-elastic and thick, became thin and elastic in the derivative species and easily distendable.

The indicated changes, first in the maternal, then in the daughter organism were accompanied by new adaptations, which originated in the gonads of the mother organism and which were expressed in the abortive destruction of eggs. The eggs that die in early stages of development are later eaten by the larvae. In connection with the new changes of the daughter organism appeared: the mesenchyma of the embryos of *Lineus ruber* possesses cellular appendices and is contractive, while the pharynx has received a greater aperture and has become shorter. The indicated changes in the structure of the embryo make it possible for it to swallow the eggs that have ceased to develop (see also below, p. 18).

From the given cases, it is seen that with the transformation of a non-larval type of development into an encapsulated larval one, the maternal organism thanks to the adaptations it has formed to link it with the daughter organism, possesses environmental characteristics and in this manner influences the evolution of the embryogenesis of the daughter organism.

Supported by the observation noted above, one can show that in any given case of non-larval and encapsulated larval development, the adaptations, which develop in the mother organism, possess the qualities of an environment. Thus, for example, the mother organisms of birds form enormous egg cells, containing in their plasma a yolk formed in the ovary of the mother. In the oviduct, this cell is covered with egg-white secretions and then with a fibrous cover, or egg-shell membranes, which contain a considerable amount of calcium salts. Following this process, a calcium shell is deposited on the surface of the fibrous membrane. In the course of its development, the bird fetus absorbs the mass of the egg white which penetrates into the amnion cavity (L. N. Ragozina, 1954), which gives to this non-larval type of development signs of resemblance with the encapsulated larval type.

#### Ecological Relations of the Mother Animal and the Ontogenesis of the Daughter Organism Among Placental Mammals

Viviparous birth is fairly widespread in different groups of animals.

In some cases, live birth preserves signs of the non-larval development characterized by large eggs, rich in yolk, and rather weakly expressed organs connecting the embryo with the body of the mother animal (see, for example, the investigations of the placenta of viviparous sharks according to the data of N. ten Kate, 1933). In other cases, viviparous birth leads to a considerable reorganization of the processes of embryogenesis. They are characterized by a sharp decrease in the size of the eggs, in comparison with allied egg-laying species, and highly-developed organs connecting the embryo with the body of the mother animal. Such a type of viviparous birth is common in prototracheata, marsupial and placental mammals. Among them, the placental mammals are those that have been most widely investigated; we shall therefore make use of data related to them in examining the role of the ecological relations of mature forms to the changes in the embryogenesis of the daughter organism. In the first place, we are interested in the question: do the changes in the adaptations of the mother animal influence the embryogenesis of the daughter organism? In other words, the question is posed thus: are the ecological relations of the mother animal primary and initial ones in regard to the changes in the embryogenesis of the daughter organism?

It is necessary to consider briefly the question concerning the connections of the embryo of placental mammals with the mother organism. The embryo of the placentals has complex and perfected adaptations connected with the corresponding structures of the mother animal. Different placentals differ in the place, time and means of implantation, and also vary considerably in the structure and functions of the organs connecting the embryo with the body of the mother.

An intimate link between the mother and daughter organisms is secured by the nervous and metabolic mechanisms (P. G. Svetlor and G. F. Korsakova, 1954 a, b 1957).

In investigating the evolution of ontogenetic processes, we cannot dispense with the data of paleontology. This data permits one to establish that the ancestors of the most ancient mammals (the so-called multi-tuberculata) were mammallike and mammaltoothed reptiles. We have no data whatsoever that would lead us to assume that the type of development of the reptiles of this group differed from the type of development proper to all other reptiles. One must presume that they reproduced like the other reptiles, by laying large eggs, rich in yolk. In particular, there is an argument in favor of this position, in the circumstance that all contemporary turtles have this type of development, turtles the ancestors of which were close to the mammaltoothed reptiles. It is also significant that contemporary egg-laying mammals, two genera and several species of echidna and one species of platypus, are specialized forms which have preserved a type of reproduction and development close to that of the reptiles. They reproduce by means of eggs which are very large (in comparison with those of other mammals) equal in dimension to the eggs of small lizards. The diameter of the echidna's egg is 4.75 mm., that of the platypus, 4.3 mm. These eggs, however, are sufficiently large so that, like all other eggs of an analogous telolecithal structure, they are endowed with a partial discoid segmentation, as a result of which there forms a discoid membrane in which the processes of the development of the embryo are concentrated.

Paleontological data lead us to seek the origins of the placentals in a group of Jurassic mammals, called as a group the pantotheria. From the group of the pantotheria, a branch parallel to the placentals has originated, including all the marsupials. This circumstance permits us to think that it was precisely in the Jurassic period that there arose that considerable reorganization of the reproductive organs of the mature individuals and of the processes of embryogenesis which led, on one hand, to the appearance of marsupials and on the other, to that of the placentals.

An important circumstance is that certain orders of contemporary placentals have preserved signs of a development that is primitive for their group. These primitive peculiarities are particularly well-marked among certain representatives of insectivora, among perissodactyls and artiodactyls, among certain sirenia and cetacea, among Afro-Asian Pholidota, and lemurs.

In some cases, the preservation of primitive peculiarities is common to all species of the given group; in others, only to some members of the group, while the other species show specialized signs.

Comparing primitive types with the secondary complex types has a certain significance for elaborating the role of ecological factors in the evolution of the embryogenesis of placentals. I will purposely omit types of development of intermediate significance, in which primitive signs are combined with secondary changes.

For the sake of clarity it should be said that in the evolution of the embryogenesis of placental mammals there are three main directions, characterized by the principal sources of food and methods for obtaining it by the developing embryo and fetus.

In the first, which embraces all placentals that have retained a primitive type of development, the principal source of food and oxygen for the developing daughter organism is the secretion of the uterine glands, the so-called uterine milk. This type of placenta can alter with the increase in the size of the body. In latter stages (for example, among large non-ruminative artiodactyls, bovidae and solid-horned ruminants) new additional adaptations for fetal growth may arise in the form of intraepithelial capillaries, which intensify metabolism between the mother animal and the fetus. Cows acquire

additional placentomas and extravasates. The latter are particularly significant among deer.

In the second direction, the main significance during the major part of intra-uterine development, lies in the supplying of the embryo with oxygen and food at the expense of substances diffused from the mucous membrane of the uterus (the endotheliochorial placenta according to O. Grosser's classification, the vasochorial according to G. Vislovskiy).

In the third direction in which the processes of embryogenesis are altered most radically, the direct source of nutrition is the blood of the mother animal, from which the embryo obtains food and oxygen. The placenta, in this case, represents one of the forms of the hematic or hemochorial placenta.

The first direction includes representatives of the seven orders of placentals mentioned above.

The second direction includes representatives of eight orders of placentals: the tubulidentata, the manatees (from the order of sirens), some species of bats, the beaver (*Castor canadensis*), and the African so-called jumping hara (*Pedetes cafer*) from the jerboas, the carnivores, pinnipeds, sloth, the European mole.

The third direction includes representatives of at least ten orders: the majority of insectivores, the great majority of bats, the dermoptera, the tarsiocidea (from the lower primates), the higher primates, the hyracoidea, the Elephantidae, the Lagomorpha (hares, rabbits), Ochotonidae, the majority of rodents, anteaters and armadillos from American edontata.

Before turning to the ecology of placentals, I shall compare the character of embryogenesis among the representatives of the first and third directions of the evolution of the placenta that differ most sharply from each other.

Primitive type of development of placentals	Secondarily altered type of development of placentals
1. Connection of the chorial epithelium with the mucous membrane of the uterus is formed late. Implantation superficial.	1. The connection of the embryo with the mucous membrane of the uterus by means of the trophoblast is established early. The implantation is frequently interstitial.
2. The embryonic node turns into an embryonic disk as a result of the appearance in the embryonic node of a cavity which breaks out. The wall of the cavity turns out, turning into the embryonic disk.	2. The embryonic node turns into an embryonic disk without the epithelium of the cavity unfolding (or undergoing eversion).
3. The entoderm, in the course of development, comes into contact with the internal surface of the trophoblast.	3. The entoderm does not come into contact with the trophoblast at any stage of development.
4. As a result of intensified growth, the trophoblast moves away from the entoderm and between them a large bodily cavity is formed.	4. The initial bodily cavity, from the moment of its formation, uninterruptedly increases, in certain cases filling with mesenchyma.
5. The amnion, as in the case of reptiles, egg-laying and marsupial mammals, is formed from the folds of the trophoblast and the somatopleura.	5. There occurs the so-called shish-amnion, the amnion's cavity develops from the cavity of the embryonic node, the upper thin wall of which changes into the ectoderm of the amnion.

- | Primitive type of development of<br>placentals  | Secondarily altered type of development<br>of placentals  |
|---|---|
| 6. The coelomic mesoderm, which takes part in the formation of the chorion, the yolk-sac and allantois, forms in the shape of coelomic sacs which grow into the large primary bodily cavity.  | 6. Coelomic sacs are not formed between the trophoblast and the surface of the entoderm. The coelomic mesoderm of the chorion, the yolk sac and the allantois is formed from the cellular elements which move out of the primary cavity of the embryonic disk.  |
| 7. A large, sac-like, entodermal allantois is formed. The system of allantoid vessels is formed from the splanchnopleural mesenchyma.   | 7. The entodermal allantois is rudimentary. Around it there is formed, in the early stages of development, a mesodermal mesenchyma, in which a powerful system of allantoid vessels develops.   |
| 8. A primitive allantoid placenta is formed, in which many placentals, (non-ruminant artiodactyls, non-horned ruminants--camels, lamas--perrissodactyla, cetacea, lemurs, pangolins and others) do not experience an adhesion of the chorion with the epithelium of the mucous membrane of the uterus (the so-called non-separating placenta or semi-placenta). | 8. The placenta is sharply specialized. Already in the early stages of its formation, the uterus epithelium is broken down as well as the connective tissue and the wall of the blood vessels of the uterus in the region of the placenta. In certain cases, the chorial epithelium is partly destroyed (in cases of the hemendothelial placenta described by Mossman). |

I shall now turn to the questions concerning the factors of the evolution of embryogenesis. In the given work, we are first of all interested in the question of the role of ecological relations of the mother animal in the evolution of the daughter organism.

A. Ecological Factors in the Preservation of a Primitive Type of Development. The role of hereditary factors in the evolution of the placenta is not specially examined here. One must emphasize that in studying the question as to the role of external, ecological factors, we do not at all have in mind some type of variant of contemporary Joffruism. In the evolution of placentation, the significance of both external and internal factors is clearly evident, as it is in any other case of evolution. Changes in ecological relations in a given species have a different effect depending on the type of placenta. It is sufficient to give one example. Certain insectivora, which include the most ancient representatives of placentals, have a fully-preserved primitive type of development with a nondropping placenta (an epitheliochorial placenta according to O. Grosser). The rodents, an order which appeared later than the insectivora, do not have a primitive placenta. Only a few rodents have a type of placenta corresponding to the second direction of its evolution, or in other words, an endotheliochorial placenta (the Canadian beaver and the African hare; *Pedetes cafer*, Mossman, 1957).

The influence of external factors on the evolution of the placenta is somewhat more precisely formulated as being the influence of the ecology of the mother animal over the embryogenesis of the daughter. Taking into account various factors of paleontology and paleoecology, and also the data of comparative anatomy, comparative embryology, and the ecology of modern placentals, one can accept the following positions as being established:

In the preservation of primitive relations the following factors are significant:

- a) Various circumstances which diminish extermination such as burrowing, a forest mode of life, a life in trees, a change to a life in seas or oceans.
- b) The peculiarities of the morphophysiology of the mammals of the given group.

Let us examine these positions in relation to separate cases of placentals which have preserved a primitive type of development.

1. The American mole (*Scalopus aquaticus*). In this case, it is evident that the change to burrowing of an ancestor of this mole, which had half a placenta, had a decisive significance. It can be supposed that the European mole turned to burrowing when it already had an endotheliochorial type of placenta.

2. The Pholidota. In this case, a primitive type of development was preserved, on one hand, because of an early high specialization of defensive adaptions (a complete armor of imbricated large horny plates, overlapping and having sharp edges) an an arboreal way of life. On the other hand, one should indicate the role of the rather large-dimensioned body, which will be more clearly seen in examining the factors which participated in preserving a primitive type of development among hoofed animals.

3. Lemurs. In this case, the preservation of a primitive type of development is explained, apparently, by an early change-over to arboreal life, connected with a nocturnal mode of life, which prevented the intensified extermination of the representatives of this group. This was also helped by the absence of any significant decrease in the size of the body.

4. Cetacea. In this case, apparently, the change to life in the water was important for large animals, having a primitive type of development and a primitive placenta. The pinnipeds, which turned to an aquatic mode of life on another level of evolution of the placenta, preserved the endotheliochorial placenta, characteristic for all carnivora.

Somewhat the same things that have been said about the cetacea can be said about the dugongs of the order of sirens. Presumably, the change to an aquatic medium also in this case took place with a group of animals which had a primitive type of development and a semi-placenta.

5. The artiodactyls and perissodactyls. Much in the ecological factors and particularities of morphophysiology, which facilitated the preservation of the primitive type of development and the semi-placenta, was of like nature in both groups. In both cases, a prolonged forest way of life was important, and this is preserved by many hoofed animals (swine, peccari, tragulidae, the African *Hyaemoschus*, and others) in modern times. Undoubtedly, the living in herds and large dimensions of the body also were important, particularly when these animals migrated into open terrain.

All hoofed animals give birth to young which have been carried by their mothers to a well-developed stage. Moreover, none of the hoofed animals can give birth to premature young in view of the impossibility for the latter of finding refuge in holes or in trees. The newly-born must follow after the grown-ups soon after birth. This is the reason for the high development of the motor apparatus, which is so clearly shown, for example, in the works of G. G. Vokker (1950). A prolonged carriage, connected with a slow development in the early stages, helps to preserve a primitive type of development.

The growth of the dimensions of the body helps, on one hand, to preserve a primitive type of development with other conditions being equal, and also under conditions of a clearly-defined herdlike mode of life. On the other hand, as can be seen among contemporary higher horned ruminants (the bovidae and deer), additional adaptations, altering and perfecting the placenta may become necessary.

B. Ecological Relations, Provoking Changes of the Primitive Type of Development into a Secondary Altered One.

1. A mode of life on the open terrain, where increased extermination took place.

2. The shortening of the length of the pregnancy in connection with the decrease in the size of the body.

In a number of cases, the importance of the transfer to life in an open terrain in connection with a small-sized body can be noted in regard to the transformation of a primitive type of development into a complex one, and of the semi-placenta into a placenta that falls off. As an example, one can indicate the hyracoidea, which almost all are dwellers in the open terrain (one of the species is arboreal and its development is unknown), and have a secondarily changed embryogenesis and a placenta that drops off. From ancestors close to the hyracoidea, the elephantidae have received a secondarily changed embryogenesis and a placenta that drops off.

Another example: the Macroscelididae--insectivores from the group of the Menotyphla, one of the species of which, Elephantulus myurus jamesoni became the object of the prolonged investigations of Van der Horst (1942, 1944, 1945). Besides the preservation of separate archaisms in its development, the embryogenesis of Elephantulus has secondarily changed peculiarities. The placenta of Elephantulus is hemochorial and labyrinthial.

The rodents afford interesting material for the question under examination. The most primitive placentas among them are those of the beaver and of the African "Jumping hare," Pedetes cafer. Then follows a comparatively primitive type of development among squirrels with an arboreal mode of life. The type of development of small rodents is sharply changed among marmots, fieldmice, mouselike rodents. In the last case, in connection with increased extermination, a shortening of the life cycle has taken place and a shortening of pregnancy. This led to the specialization of the embryogenesis and to the formation of a sharply-specialized placenta.

These general positions can be applied to primate and Hominidae evolution.

Modern man has the same type of placenta as the modern manlike apes. Their embryogenesis, however, have certain characteristic differences.

The particularities that characterize the embryogenesis of man are as follows:

1. A sharp acceleration in the early stages of development.
2. The oval development lasts three days.
3. At the end of the fourth day the blastocyst begins to form.
4. At the end of five days the blastocyst is formed.
5. During the seventh day implantation begins. At the beginning of implantation, the embryonic node has already undergone differentiation--the cavity has been formed and the early beginning of the entoderm has taken place.
6. Like many other placentals, with a secondarily changed placenta, the human embryo does not change from an embryonic node to an embryonic disk by unfolding.
7. The human embryo has a shis-amnion.
8. The entodermal allantois is reduced.
9. The anlage of lateral layers of the mesoderm in the region of the chorial vesicle is absent. This anlage is formed very early in the form of a syncytial mass of cells, forming on one side the magma reticulare, and, on the other, a layer of cells, which underlie the trophoblast and as a result of which the trophoblast is turned into a chorion.

Among other peculiarities, the acceleration of development in the ante-implantational stages should be indicated. While in macaques, the beginning of implantation takes place at the end of the 9-day period, in man, according to the assumption of Hertig and Rock (1945), the beginning of implantation is placed at the end of 6 days. The embryo, at an age determined as 7-7½ days, is already in a rather late stage of implantation. The implantation of a human embryo begins 2 or 3 days earlier than that of a monkey--the macaque.

As far as the anthropoid ape, the chimpanzee, is concerned, the aggregate of all morphological signs shows that the embryo, the age of which has been rather precisely determined as 10½ days, corresponds to the human embryo at the end of 9 days. Thus, the human embryo surpasses, in the early stages of implantation, the development of the embryo of the chimpanzee by 1½ days.

This peculiarity of man--an accelerated development in the ante-implantational stages and in the stages of early implantation--may also be connected with his conditions of existence. It is possible to think that the decisive condition in the given case is walking erect. Under the conditions of walking erect and the other morphophysiological particularities of man (single birth, a small uterus with a cavity comparatively limited in size during the time of implantation) an early implantation decreases the danger of placental presentation, that grave complication which requires surgical intervention.

The development of the human embryo during later stages, beginning with the twentieth day, slows down. Partly, this may be connected with the condition of the growth of the primary cavity of the trophoblastic and chorial vesicles during the stage from the 11th to the 20th day and following the appearance of the anlage of the nervous plate and its transformation into the nervous tube.

Let us compare the development of man with the development of the embryo of a cow. With gestations almost equal in duration, developments during the first month permit the distinguishing of diametrically opposed processes. The cow's development during the first half of the month is distinctly slower in comparison with man's. By the 20th day, both cases reach the stage of the nervous plate. Then, the development of the embryo of the cow proceeds more quickly. This is shown by the following table.

	Early Embryogenesis of Man	Early Embryogenesis of the Cow
The segmentation of the egg in the oviduct	less than 3 days	4 days
The beginning of the formation of the cavity of the embryonic node	7 days	13 days
Formation of embryonic disk	12 days	end of 14 days
Formation of nervous plate	20th day	20th day
Stage of 25 somites	28 days	less than 24 days
Stage of 28 somites	30 days	24 days

The marked slowing-up in the development of the human embryo during the last third of the first month cannot be attributed to the organs, which supply the embryo with food and oxygen. These organs constantly develop and are proportionately far more powerful than with the embryo during the stages of early implantation. It is sufficient to indicate that the human embryo at the end of the first month of development has 28 pairs of somites while the cow embryo at the age of 30 days has its full complement of 46 pairs of somites.

The last observation relates to the general periodization of intra-uterine development. In this case, it is also convenient to compare the periodization of the intra-uterine development of the cow, as a placental mammal, which has a gestation close to that of man in duration, but which varies sharply from man's in the type of embryogenesis and the peculiarities of placentation.

As is known, the author proposed (1954, 1955) that three principal periods be distinguished in intra-uterine development: (1) embryonic, (2) pre-fetal, and (3) fetal. The embryonic period in man is very long as compared with the cow's: 45 days for man and 34 for the cow. Likewise, the pre-fetal period is somewhat longer, lasting 30 days with man. The fetal period, holding that the average length of pregnancy in man is 274 days (Stark, 1955 a,b, 1956) while the cow's is 284 days, lasts in man from the middle of the third month (the age of an early fetus is 75 days) to the beginning of birth, that is 200 days, while the cow's is about 225 days.

As can be seen from what has been said, the level of our knowledge permits us to grasp, in separate cases, a connection between the conditions of existence of the ancestral forms and the retention of primary relations or the appearance of secondary changes. There undoubtedly exists a connection among placental mammals between the ecological relations of the mother animal and the ontogenesis of the daughter individual.

Based upon an examination of the entire material of the first part of the present work, the following general conclusions can be made:

1. The change of one type of embryogenesis into another may take place on the basis of adaptive changes in the early stages of development in cases of free larval development, when in early stages, the daughter organism already has independent adaptive relations. In other cases, the adaptive changes in the mother, by means of the connections between it and the daughter, are reflected in the processes of embryogenesis of the daughter.

2. What reacts most energetically on the adaptive changes of adult individuals are those organs and their anlagen which, in early embryogenesis, possess independent adaptive significance.

3. By studying the morphophysiological peculiarities of adult forms, their ecology, the adaptive relations in embryonic development and the processes of early embryogenesis, one establishes the chain of causal relationships. It leads from the primary changes in the ecology of adult individuals to the changes in their biology of reproduction, which are followed by changes of these processes of embryogenesis which have a direct adaptive importance, and finally, changes in their permanent organs.

4. In all examined cases, together with ecological factors, the importance of morphophysiological peculiarities of the animals was discovered.

5. In principle, the same path is apparent in the changes in the processes of embryogenesis in a complex type of development with viviparous birth among placental mammals. This is seen, for example, in the transformation of a type of embryogenesis primitive for placentals into a secondary, specialized type. With this also, the initial source of the changes is the change in the ecology of adult organisms (for example, a change from life in forests, that is, under conditions of cover, to life in open spaces) frequently connected with changes in their morphophysiological peculiarities. Adaptive changes in adult organisms bring forth the necessity of changes in the embryogenesis of the daughter, and, in the first place, precisely of these organs and their anlagen, which are linked with adaptation under the conditions of development within the uterus (the trophoblast, the means

of its development, the means of the formation of the amnion, the means of implantation, the development of the yolk sac, the formation of the allantois, and others). The development of permanent organs alters in dependence on provisional organs...

#### Ectogenic Factors of Ontogenesis

The participation of the environment in the ontogenetic formation of the form can be presented at a minimum in the form of three categories of events.

In events of the first category, the environment represents a totality of conditions necessary for the realization of the given ontogenesis. In the case of the laying of eggs by terrestrial animals, the number of indicated conditions includes the temperature and humidity of the environment, the quality of the substratum, etc. In fresh water, significant conditions include the degree of cleanliness of the body of water, the slow or fast rate of flow of the water, the character of the bottom (when the egg is deposited at the bottom), conditions of aeration, etc. For sea animals, the composition of the sea water in which the embryo develops, is important. In this case, numerous authors have shown particularly clearly that development takes place in the closest connection with the environment. Changes in the composition of salt water lead to disturbances in the formation of the embryo.

The second category of events includes the direct participation of separate elements of the environment in ontogenetic morphogenesis. At first glance this category is close to the first one. However, the line of separation here is the fact that in the first case the environmental factors do not determine the course of ontogenetic morphogenesis, although it is disturbed or altered when those factors are altered. In the second case, the factors of the environment have a direct relation to morphogenesis.

The third category includes cases of correlative connections of adaptive organs with those organs and anlagen which do not have an independent adaptive significance. This category also includes the connections of ontogenetic morphogenesis. But, at the same time, something begins to be seen regarding the question of the specific factors of morphogenesis. In the "lithium development" the entodermization of the ectoderm can be observed, with the formation of exogastrulas. This disturbance indicates something new in the interrelations of the ectoderm and entoderm, of the animal and vegetative poles of the axial gradient.

For early morphogenesis, we know two generalizations--the axial gradients of Child (1929, 1941) and the organizational centers of Speman (1918, 1936). The source of the axial gradients of Child is in the primary relations of the organism of lower animals to the environment in early stages of development. The system of axial gradients is older than the system of contact interactions, about which we first learned in the words of Speman.

Certain processes of the early stages of development, which have been prepared already in the course of ovogenesis, should be, apparently, also examined while taking into account axial gradients. Thus, for example, the author (G. A. Shmidt, 1941) observed curious processes of the concentration of plasmic substances in connection with the maturation fission of the primitive leech Protoclepsis tesselata O. F. Mill. As a result of this concentration, there is a system of axial relations with two culminative points--the formation of the so-called ring and of the vegetative disk, connected by a network of plasmatic streaks.

In the process of segmentation, these plasmas become distributed in a regular manner. The main mass of the animal ring goes into the primary

ectodermal teloblast, and almost the entire mass of the vegetative plasma disk is mixed into the primary mesoblast. The plasmic substance of the ring and disk is distributed among the blastomeres--the descendants of the primary ectodermal teloblast and of the primary mesoblast.

Probably, the system of axial gradients should also be mentioned in connection with the widely-known observations of Conklin (1905) on the distribution of variously-colored plasmic substances in Styela partita. The distribution of these substances, linked with the maturation of the egg, is subordinated to a definite plan, linked with subsequent processes of segmentation.

A connection has been established among vertebrates between substances that are formed during ovogenesis and the morphogenital system of the embryo. Like the transference of substances in Styela partita, the transference of substances, accumulated in the plasma of the egg during ovogenesis, is tied here with the phenomena of maturation and fertilization. Even before the beginning of segmentation among tailless amphibians, there is an easily-noticed plasmic mass, the "grey sickle" or "grey crescent," which stands out by its color and structure from the rest of the mass of the animal pole.

At the same time, in the latter case, one can observe the replacement of the system of axial gradients by a new system of contact correlations. This is seen from the fact that the substance of the grey sickle goes into the anlagen of the chorde-mesoderm, which is the center of the early morphogenetic system of the embryo. It enters into the composition of the so-called primary organizer, which induces a nervous layer in the ectoderm.

One may suppose that similarly to the fashion in which the phylogenetic basis of the system of axial relations was composed by the primary relations of the metabolism of the organism with its medium, the phylogenetic basis of contact interactions was composed by the primary morphological relations with the medium, which later became a system of morphological contacts. The primordial participation of the environment in the morphological system of early ontogenesis is indicated by the fact that the initial source of the formative action is the outside embryonic sheet, or its derivatives, the nervous tube, the optic vesicle, hearing vesicle, nasal cavity, etc.

The two enumerated systems of early ontogenesis may coexist--which can be deduced, for instance, from the fact that the nervous layer and nervous tube are a substantive part of the system of gradients and, at the same time, are the inductors of many anlagen.

b) Morphological Influences of the Environment on Larval Stages of Development and on Half-mature States.

From the experiments of A. A. Mashkovtsev (1935, a, b, 1936, 1940) on the larva of amphibia, the role of oxygen (and perhaps of CO<sub>2</sub>) as a morphological factor of the environment can be deduced. Mashkovtsev showed that there are three types of morphogenesis of the lung among amphibians. With one of them, the most primitive, the axolotl, larvae brought up under a metallic net over the surface of the aquarium, do not produce an alveolar structure of the lung as do the controls. A repetition of the same experiment with the tadpoles of grass and edible frogs and chesnochnitsa (a species of frogs with a faint, garlic-like odor<sup>Tr.</sup>) indicated that in this case the lung, even when the larvae are brought up under a metallic net, attains the stage of transverse fragmentation. A full fragmentation takes place, according to Mashkovtsev, "under the influence of inspiration and expiration"; the alveolar structure of the lung of the axolotl develops under the influence of the function of respiration.

Among toads, the complete fragmentation of the lung occurs without the participation of the act of respiration. Keeping tadpoles under a metallic net creates no obstacle to the fragmentation of the lung, which, before the first breath, is markedly fragmented, swollen with serous liquid and has the appearance of a bunch of grapes. In the course of the larval stage, the tadpoles of toads have the cavity of the lungs separated from the mouth cavity by an epithelial stopper of the rima glottidis. Only after they crawl out on land, as a result of a rather lengthy accumulation of carbon dioxide in the blood, the smooth muscles strongly contract. The serous liquid is expelled from the lungs through the torn epithelial tissue which had closed the rima glottidis.

Curiously, the young of the oviparous mammals that have just come out from the protection of their egg-shell, and newly-born marsupials, according to the data of Narath (1896) both have undeveloped lungs, with only the basic bronchi. Their blood vessels serve for the exchange of gases during respiration. Very soon after breathing begins, an intensive branching of the bronchi takes place together with the formation of alveoles at their ends.

In the placentals, the lung is already formed at birth. According to A. I. Strukov's data (1932) children, up to the age of seven, undergo the formation of new, small bronchi, bronchioles and alveoles. After seven, the lungs are completely formed in regard to their structures.

Differences in the course of the morphology of lungs among tailed and tailless amphibians, in connection with different participation of the morphological factors of the environment, to a certain extent, can be connected with their phylogenesis (Smalhausen, 1957). Tailed amphibians have retained a more intimate connection with water than the non-tailed ones and are adapted to a lesser degree to a terrestrial mode of life. The tailless amphibians have more markedly defined characteristics of land-dwellers. Among our amphibians, the toad is most particularly a land-dweller. Mashkovtsev, as indicated above, found that its differentiation is easily performed with the exclusive help of morphological mechanisms, rooted in the organism itself of the toad.

One must call attention to another side of the same morphological process. As has been stated, the retention by tailed amphibians of more primitive ecological relations (and of a somewhat more primitive organization) than that of the tailless has an important significance. On the other hand, the lung is a "new" organ for amphibians. It first appeared in a primitive state among representatives of this class. The abdominal air bladder of the common ancestors of the dipnoi, polypteridae, crossopterygii and earth-dwelling vertebrates can only be taken as an original formation.

This moment should probably be taken into account in investigating other organogenesis both of the amphibia themselves as well of other vertebrates and invertebrates. Thus, for example, among the "new" organs of reptiles, are a scaly skin, the thoracic cage, a secondary kidney. "New" organs among the class of birds are feathers, a four-chambered heart with a right arch of the aorta, air sacs. Among mammals, the "new" are a hair cover, the apparatus of cutaneous glands, and, in particular, the mammary gland, alveolar lungs.

In like manner to the loss among the most terrestrial amphibians, such as the toad, of the connection with the environment in the differentiation of the lung, it is very likely that it will be found that many other contemporary reptiles have lost their linkage with the environment in the differentiation of their secondary kidney or the thoracic cage. It is more likely that

a connection of organogenesis with the morphological factors of the environment will be found among archaic forms, such as the hatterias, among reptiles, the hoatsin or tinamu among birds, the platypus or echidna among mammals.

Among amphibians, we are familiar with another fact of the participation of the environment in morphogenesis. That is the discovery of Witschi (1942) of the effect of temperature on the formation of sex. By increasing the temperature, he succeeded, in a very significant manner, to alter the number of larvae which turn into males.

c) Replacement of Morphogenetic Factors of the Environment by a Source of Morphogenesis Within the Organism of the Animal.

The question of the replacement of morphological factors of the environment by sources of morphogenesis belonging to the organism issues from the comparative study of various morphogenesis taking place with the help of endocrine glands. Among them are the experiments of A. A. Mashkovtsev, which were mentioned in the preceding section. Mashkovtsev, himself, under the influence of the views of Roux (1920) allots the greatest importance to the functional moment--the respiratory movement in the differentiation of the lung tissue. The mention of oxygen is made in passing while examining the role of the respiratory movements--inhalation and exhalation. However, there could hardly be any objections to these and other experiments being examined from another point of view. This point of view is the concept of the replacement of a morphological environmental factor, specific for the given organism, by another factor belonging to the organism itself.

The views of Roux are in the given instance one of the first attempts to indicate the general factors of ontogenesis. This attempt cannot be called a successful one. According to Roux, three stages must be distinguished. In the first of these, the development of organs takes place under the influence of internal factors placed in the embryo or in its separate anlagen. In the second stage, the organism continues its development under the influence of internal factors, but then acquires certain differentiations under the effect of trophic functional irritants. In the third stage, according to Roux, develop under the influence of only functional irritants.

It is natural that Roux' expositions, made prior to the works of Spemann and many other experimental embryologists, prior to the modern conception of nervous and hormone secretions, prior to the foundation of the ecological direction in embryology are open to criticism.

One must underline that in the generalizing article of Mashkovtsev the tendency is seen in different places to liberate himself from the obsolescent views of Roux. However, Mashkovtsev did not arrive at the correct point of view. More than that, he attempted to generalize the views of Roux, developing the idea of three phylogenetic stages lying at the bases of the three stages of ontogenesis according to Roux.

Certain data, obtained from experimental works, related to the period of incubation, permit one to see more clearly the correlation of the physiological and morphological functions.

The Italian investigator Remotti (1933) showed that the density of the capillary network of the allantois depends on the partial pressure of the oxygen in the incubator. With an increased partial pressure of oxygen, higher by 50-70% than normal, applied from the 2nd to the 7th day of incubation, the capillary network of the allantois is found to be less dense than usual. In this case, oxygen acts as an original inhibitor of the development of the capillary network, which develops intensively apparently in answer to the well known difficulty of the embryo in obtaining a sufficient supply of oxygen.

According to the data of A. L. Romanoff (1952) the capillaries of the allantoid vascular field do not develop if the allantois does not come into contact with the serosa (the chorion).

The Italian investigators Osseladore, Pezzuoli, Pietri (1954) showed that under conditions of an excess of oxygen in the blood, Botal's duct shuts. The introduction of Ringer's solution saturated with oxygen, into the blood stream of the fetus of the guinea pig effects the contraction of the walls of Botal's duct. On the contrary, the dilatation of its walls was obtained by the introduction of Ringer's solution, saturated with carbon dioxide. Alternating contraction and dilation of Botal's duct was obtained 4-5 times in succession with the same guinea pig. The above-mentioned authors come to the conclusion that the increase in the saturation of blood with oxygen after the new-born begins to breathe with his lungs produces the functional closing of Botal's duct.

The data given above have a certain interest in regard to the question on the correlation of functional and morphogenetic factors. The first are related to the category of conditions that ensure the flow of the ontogenetic morphogenesis. At the same time, one can see that between both categories of events there is no complete separation, but, on the contrary, they are connected--one ensures the other.

In the experiments of Remotti and Romanoff, conducted with bird embryos, of Osseladore, Pezzuoli and Pietri with the fetuses of guinea pigs, oxygen is a physiological and not a morphogenital factor. The physiological effect can completely inhibit morphogenesis. A badly formed vascular field of the allantois will be unable to meet, in later stages of development, the demands that should be met by the vascular network. The physiological factor can alter the course of the morphogenital process, if, for example, an insufficiently developed vascular network provokes a delay in the development of an organ, or if it leads to other infringements of the course of development (an assymmetrical development in paired organs, the reduction in size of the organ, for example, of the kidneys, etc.). At the same time, both categories of factors are qualitatively separate, although they have multiple links with each other.

In A. A. Mashkovtsev's experiments concerning the morphogenetic process of the differentiation of the lung, oxygen appears as one of such morphogenital factors (perhaps CO<sub>2</sub> likewise). In toads, this factor is replaced by another, which belongs not to the environment but to the organism itself--thyroxin of the thyroid gland.

Sembrot's experiments (1954) are very interesting. Their results, it seems to me, show an important moment in the evolution of morphogenesis.

In a number of experiments Sembrot showed that the endostyle of the lancelet had the capacity of bringing about the metamorphosis of the axolotl into an ambliscoma. The implantation of between 10 and 20 dried endostyles of the lancelet brings the appearance of pulmonary lytic processes. With the implantation of 30 endostyles, signs of the metamorphosis appeared on the 13th day after the operation. With the implantation of 40 to 65 endostyles, the process of metamorphosis began 5-7 days after the operation. As a control, other axolotls had implanted in them dried tissue of the muscles of the tail of the lancelet, which did not provoke any metamorphosis.

The homology of the endostyle and of the thyroid gland has been noted more than once. The early anlage of the thyroid gland in all vertebrates is unpaired and is represented by a pitlike sinking of the bottom of the front part of the pharyngeal tube. In its position this hollow corresponds with the sulcus-like anlage of the endostyle of larvae of the lower chordates.

Sembrot's experiments show that the endostyle which, in the lancelet, has as its principal function the mixing together of food particles which fall on it from the sea water, has, at the same time, the auxiliary function of a ductless gland.

These experiments permit the following supposition: The organs that later came principally to function as endocrine glands, originally had a closer and more direct connection with the environment. Only later did they become isolated from the environment. At the same time, a morphogenital system was created, based on a direct genetic connection with the environment.

Just as Drish made an unsuccessful proposal to replace the expression "mechanics of development" by "physiology of development," in order to avoid confusion it is better not to use the expression "function" when talking about morphogenesis. Morphogenital functions are qualitatively unique and to mention function only hinders the understanding of that important circumstance. Consequently, the system of endocrine organs are in a special place, just as are the regions of the brain, which have a neurocrine secretion. The products secreted by endocrine glands are of a special kind as is their function: the products that are secreted by the endocrine glands are morphogenital factors.

The most important theoretical significance is the replacement of one morphogenital factor by another. It is precisely this conception that allows us to say that ontogenesis is not autonomous.

A. A. Mashkovtsev writes at length that, in the third stage of phylogenesis, a complete automatization of morphogenesis is reached, "the process of determination descends to the earliest stages of development (mosaic segmentation"). It is obvious that in speaking about "mosaic" segmentation, A. A. Mashkovtsev has in mind any kind of segmentation in which the early determination of the anlagen of the organs takes place.

The following section will show that also "mosaic" segmentation is indirectly linked with the system of adaptive relations.

Another moment with an important theoretical significance should be noted. A direct morphogenital connection of the organism with the environment during embryonic stages, as can be seen, cannot be preserved for long. The replacement of the morphogenital environmental factor in the development of the lungs that occurs in axolotls by an endocrine factor in toads appears to constitute a typical phenomenon.

The morphogenital connection with the environment is preserved where the morphogenital phenomena are linked with seasonal phenomena. In this case, the natural factor to the largest extent ensures the realization of the morphogenital processes. It contributes to the fulfillment on time of tasks important for the species.

The works of Rowan (1925, 1938), Bissonette (1931, 1935) and of others showed that light is a stimulant of spermatogenesis in birds. Placing a hood over the head of the bird stops light from shining into the eyes and provokes a check in spermatogenesis.

Recent investigations of Jacques Benoit (1952) indicate the path of the connections of the optical nucleus in the hypothalamus with the front part of the hypophysis. The production of neurosecretion by specific cells of the hypothalamus is conveyed through small vessels into the front part of the hypophysis, stimulating the formation of gonadotropin, which in its turn stimulates the formation of sperm.

The Participation of Environmental Factors in the Ontogenetical Morphogenesis Through Correlative Links.

A. Means for the participation of the environment in ontogenetic morphogenesis.

The environment can participate in ontogenetic morphogenesis by means of correlative connections between the anlagen of separate organs.

The generalized meaning of the cases of morphogenesis under examination consists in that in addition to phenomena of direct participation of the environment in ontogenetic morphogenesis, there are a series of other types of connections between the environment and the developing organism, which indicate that the participation of the environment by different roundabout and indirect ways is deeply imbedded in various sides of individual development.

Several groups of similar morphogenital connections should be distinguished

1. The influence of changes in provisional organs on the ontogenesis of definitive ones. For example, the connection between differences in the means of nutrition of two species of shore nemertini, Lineus desori and Lineus ruber and the development the pharynx and proboscis. In the initial type, Lineus desori, all the embryological development takes place at the expense of the yolk, formed in the egg plasma during ovogenesis. The pharynx among embryos of this species does not function in the course of embryogenesis and is subject to reduction. The proboscis develops at an intensified tempo and when the nemertini hatch out of the eggs, it is of large dimensions and well diversified. In the secondary type, in addition to the yolk, formed in the egg plasma during ovogenesis, there is additional nutrition for the larva in the form of abortive eggs. The pharynx of the embryos and larvae of this species does not degenerate and is well developed at hatching time, while the growth and development of the proboscis show a definite slowing-up. At the moment of hatching, the proboscis is considerably smaller than in the nemertini of the original species, and clearly lags behind it in its differentiation.

2. Changes in the earlier stages of the processes of ontogenesis, which do not have an independent adaptive significance depending on changes in organs having an adaptive significance. For example: the changes in the peculiarities of the spiral segmentation in relation to falling out of the plankton larva of the trochophore (P. G. Svetlov, 1922, G. A. Shmidt, 1930-1941). The processes of segmentation, leading in their later stages to the formation of the organs of the trochophore, do not have an independent adaptive significance. The evolution of the processes of segmentation proceeds on the principle of indirect adaptation: alteration or reduction of processes of segmentation takes place depending on the evolution of the organs of the trochophore--their reduction or alteration.

3. The influence of adaptive alterations of organs upon the middle stages of embryogenesis. The falling out of the trochophore leads not only to the alteration of processes of segmentation but also to the change of the so-called "middle stages" of development (something like the deviations of A. N. Severtsov and F. Muller), for example leading to the appearance and high differentiation of teloblastic organogenesis of ectodermal organs. Teloblastic organogenesis of ectodermal organs can be examined as an adaptation to a shortened development. It is provoked by the need for an earlier formation of the nervous and muscular systems in non-larval development, in which all the food that is necessary for the processes of embryogenesis is contained in the egg plasma, and is not obtained by a lengthy process from planktons, as is the case in trochophore development.

4. The influence of adaptive changes in early stages on the subsequent course of development of corresponding organogenesis. The symmetry of the total structure of the plankton larva of the higher group of unarmed nemertini (the pilidia) is reflected in the definite and symmetrical disposition of the anlagen of definitive organs. The adaptive peculiarities of the plankton larva of the pilidia, the type of its symmetry and other signs are reflected in the consecutiveness of the development and the distribution of definitive anlagen—embryonic disks. That we are talking of a stable inherited sign can be seen from the fact that the same type of symmetry and the same consecutiveness in the appearance of embryonic disks have been preserved also after the pilidium has vanished in the nemertini Lineus desori, which have a non-larval type of development (G. A. Schmidt, 1932, 1941, 1956).

5. Links between the early stages of development and subsequent processes of embryogenesis. In this case, I shall examine the question concerning the primacy of processes of development in placental mammals, which have a primitive type of development.

B. The chain (or graduated) character of the connections between the processes of the inner cellular mass in early embryogenesis in placental mammals.

The question as to how the initial change began is not examined here, in view of the still great lack of clarity of this question, which is in part attributable to the sporadic character of observations of the development of these groups, which could to the greatest extent contribute to clarifying this question. Thus, data on the beginning stages of embryogenesis in the American mole Scalopus aquaticus, which has a primitive type of development, are completely lacking. Also lacking are data concerning the large, aqueous insectivore from Western Africa—the Potamogale velox. Available data are concerned with objects, the development of which is considerably altered: Elephantulus myurus jamesoni and the Hemicentetes semispinosus. I shall limit myself therefore to examining the given question—the character of the dependence among separate links of embryogenesis. These links are the following:

a) The formation of a one-layered cellular sphere, from which the trophoblast develops, and a prolonged non-entry into the wall of this sphere of the anlage of the embryonic part (which adjoins to the trophoblast from inside), as a means for the rapid and considerable growth of the blastocyst and of the trophoblastic vesicle.

b) The appearance of a formation specific for placentals—the inner cellular mass, as a process depending on the formation of the cavity anlage of the trophoblast.

c) The unfolding of the inner cellular mass and the coming out of the anlage of the embryo into the common superficial layer of the embryo together with the trophoblast at a comparatively late stage of development.

d) The porous contact between the trophoblast and the entoderm, as means for forming the large primary cavity of the body.

e) The formation of the latter, as a prerequisite for the growth in it of the coelomic sacs.

f) The formation of the large coelom, as a direct prerequisite to the formation of the saclike allantois. Its growth under the chorion and a contact with it which takes place result in the formation of the primitive allantoid placenta.

The general character of the succession of the processes of embryogenesis may be defined as a chain of or graduated correlations.

I shall note that the questions given above are at the same time the central problems of the early embryology of placental mammals (G. A. Shmidt, 1959).

In the given case we are interested in the question on the connection existing among separate processes of early embryogenesis, which begin with the reconstruction of initial stages, which leads to the appearance of the atypical blastocyte, which is the beginning stage of subsequent changes leading to the formation of the allantoid placenta at rather early stages of development. One of the changes that take place in connection with this, in which respect the placentals are sharply distinguished from the marsupials, is the disappearance of the egg shell, which exists in the oviparous and the marsupials and which is absent in placentals. We do not know what changes in the ecological relations have provoked the disappearance of the egg shell, but there can hardly be any doubt that it is precisely this adaptive alteration that became the prerequisite for all subsequent changes in the early stages of embryonic development.

As is known, the basic difference in the initial stages of the embryogenesis in marsupials and placentals is, in marsupials, a complete blastula, the wall of which consists of a single row of cells. In the marsupial Dasyccrus viverrinus, J. Hill, 1910, found that such a blastula or, as he calls it, a blastocyst in marsupials can be divided into two hemispheres—the animal and vegetative, from which the first, according to Hill, the "formative" one, turns into the anlagen of the embryo itself while the second is the anlage of the ectoderm of the serosa, which is called by Hill a trophoblast, in analogy with the placentals.

The processes of initial embryogenesis in marsupials, their segmentation and the formation of early embryonic anlagen are in substantial features close to the oviparous in spite of marked differences in the size of the eggs.

The essence of the radical reconstruction of the processes of segmentation and the formation of the first embryonic anlagen in placentals is (G. A. Shmidt, 1959) that the trophoblast takes the center of the stage: its basic structural features are formed in the first place at the time when the anlage of the embryo in the form of a formation, specific for placentals, of an inner cellular mass appears following the trophoblast. It is this, precisely, which must be accounted as the specific particularity of the beginning stages in the development of placentals (see the analysis of the data of Heuser and Streeter, 1929, on the segmentation of the egg of the domestic swine, the data on the segmentation of the egg of Hemicentetes semispinosus, G. Blunchli, 1937, a b, and the data of Van der Horst, 1942, on the segmentation of the egg of Elephantulus myurus jamesoni in the indicated work of the author, G. A. Shmidt, 1959). It is precisely this way that there arises a typical blastocyst, in which all the external cellular wall is the trophoblast, inside of which is disposed the inner cellular mass.

In the further course of the evolution of ontogenesis the perfecting of this said process of differentiation of the first two anlagen led to the fact that the differentiation of the external anlage of the trophoblast and the central anlage—the internal cellular mass—takes place in a solid morula-shaped stage until the formation of a cavity in anlage of the trophoblast. In this later type of segmentation in placentals, the cavity appears between the two stated anlagen after both anlagen have been differentiated.

The most important significance of the appearance of an atypical blastocyst in placentals lies in the fact that the total increase in the dimensions of the vesicle-like embryo depends from a single anlage of the trophoblast. However, there is another important angle to the significance of the indicated marked change: the yolk sac, which among marsupials is either an absolute obstacle to the formation of an allantoid placental or, at the most, leads to the development of only a small allantoid placental, among placentals, as result of the said reconstruction, ceased from being such an obstacle. This circumstance will be clearly seen from further exposition.

b) Transformation of the internal cellular mass into an embryonic node. In the primitive embryogenesis of the cow, as studied by the author, after the differentiation of the two first anlagen, the trophoblast and the internal cellular mass, the next, second, nodal process of early embryogenesis consists in the transformation of the internal cellular mass into an embryonic node and into an anlage of the ectodermal mesenchyma. In the stated subject, three days pass from the differentiation of the internal cellular mass to the final formation of the embryonic node.

Subsequent processes during the stages of the blastocyst consist in the formation of the entoderm, the principal, of not only, source of which is the internal cellular mass, and, particularly, the embryonic node which is formed from it. The formation of the entodermal vesicle, that is, of the layer of cells disposed internally from the trophoblast, is completed in early stages of the blastocyst, which has an embryonic node, after which an intensified growth of the blastocyst begins, leading to the freeing from oval membranes of the yolk membrane and the clear membrane.

c) The transformation of the embryonic node into an embryonic disk. The third nodular process of embryology consists in the transformation of the embryonic node into an embryonic disk. This process is prepared by changes in the embryonic node during the stages of the later blastocyst. Even though the vesicle-like embryo continues at these stages to be covered with oval membranes, nutrition from uterine milk penetrates into the trophoblast and the latter ensures the assimilation of all the nutritive substances and their transmission to all the embryonic anlagen. During the late phase of the blastocyst, the diameter of the embryonic node increases from 26  $\mu$  to 130  $\mu$  and higher. The structure of the embryonic node also alters significantly. From a small group of large, blastomere-like cells there rises a bigger group, consisting of small cells, disposed in the cow embryo in the shape of two cellular plates--the smaller, on top, and the larger, below.

After it is freed from oval membranes, a cavity appears in the center of the anlage of the embryonic node. The dimensions of such a vesicular, trophoplasic bubble begin rapidly to increase. In the second half of the 14-day period, the cavity of the embryonic node bursts out and the unfolding of the two plates begins into a common anlage of the embryonic disk. Beginning with this stage, the anlage of the embryo--the embryonic disk--is situated in the same outer plate of cells as the trophoblast.

d) The formation and growth of the primary bodily cavity, as a prerequisite to the appearance of the large coelomic cavity. Those placentals who have a primitive embryogenesis, that is, artiodactyls and perrissodactyls, certain insectivora, certain sirenians, cetacea, Pholidota, and lemurs, form a large coelom in the region of the organs of connection

with the body of the mother animal. There arises the natural question as to the prerequisites for its formation. This question is apposite first of all because in cases of primitive embryogenesis a large, entodermal allantois is formed, which could not appear without a sufficiently large coelomic cavity.

After the embryonic disk has attained a certain level of growth and differentiation, which is expressed outwardly by the appearance of the primary cavity, and the trophoblast also significantly has increased in size, there begins, at a certain level of development, an intensified growth of the trophoblast, as a result of which the trophoblast moves away from the entoderm and the formation takes place of the primary, growing cavity of the body.

If the cow embryo is taken as a concrete subject of development, then after the formation of the embryonic disk at the end of 14 days and up to the middle of the 15th day, the growth of the entoderm proceeds in a parallel fashion with the growth of the trophoblast. The intensification of the growth of the trophoblastic vesicle during the 16th day leads to the fact that the trophoblast begins to grow considerably more strongly than the entoderm. Since the connection between the trophoblast and the entoderm is not firm, the trophoblast begins to move away from the entoderm and there appears between them first a small fissure, then a swiftly-growing primary cavity of the body. Already at the end of 16 days, it becomes sufficiently large so that anlagen of coelomic mesoderm from the primary cavity grow in it. These anlagen are symmetrically disposed on the sides from the symmetrical plane. Soon, on the distal side of the anlagen one can notice the coelom being formed. In the course of the 17th day, the coelomic cavity becomes rather large. During the 18th and 19th days, the exterior leaf of the mesoderm enters into a close contact with the interior surface of the trophoblast, and the internal leaf (the splanchnopleura) tightly adheres to the surface of the yolk and sac.

e) The formation of a large coelom, as a direct prerequisite to the formation of a large, saclike entodermal allantois. The fifth and most important nodal process, which ensures the formation of a powerfully developed allantoid placenta, consists in a considerable increase in the size of the coelom, which pushes out the primary bodily cavity. The formation of a firm contact of the somatopleura with the trophoblast and of the splanchnopleura with the yolk sac continues in the subject investigated by the author (the cow) up to the end of 20 days.

At the end of 20 days the early anlage of the allantois becomes noticeable in the cow at the stage of an embryo with 7 pairs of somites. The same stage is indicated for the domestic pig by Heuser and Streeter (1929). The allantois in its early stages grows rather slowly. Only after 2-3 days after its formation, does the allantois, filling with transudate, become so large that it comes into contact with the internal surface of the chorion by means of the leaflets of the coelomic mesoderm.

Later, the saclike, entodermal allantois grows intensely (in the cow, about 3 cm per 24 hours), increasing both in length and in thickness. In artiodactyls, we notice a considerable increase in the dimensions of the entodermal allantois, which has a sausagelike form, corresponding to the form as a whole of the embryonic and prefetal vesicle, and completely justifying the appellation given to it. Particularly significant is the increase in the absolute dimensions of the allantois in the cow in the course of the second month, during the prefetal stages, when the total length of the entodermal allantois at the end of the second month may reach 1 meter in length and 3 cm in thickness.

Such, in its essential features, is the consecutiveness of the processes, which ensure the formation and the free growth of the saclike allantois, which makes possible the formation of the allantoid placenta.

All that has been exposed in the given article makes it possible to make certain preliminary conclusions:

The course of the evolution of ontogenetic processes has an adaptive character. It is linked with changes in the ecological relations of the organism of the given species.

2. The evolution of embryogenesis can be significantly affected by adaptive phenomena in early stages of development, particularly in cases of free larvae.

3. In non-larval development, the mother organism acquires the significance of the environment in the evolution of the ontogenesis of the daughter. Alterations in the ecological relations of the mother animal lead to alterations in the embryogenesis of the daughter (for example, in the change of habitation by ancestors of the nemertini Lineus desori to the lower horizons of the bare shore).

4. Alteration in the ecological relations of the mother animal in placental mammals also leads to alteration in the embryogenesis of the daughter.

5. The basic sources of morphogenital influence belong to the organism itself. It would be a mistake, however, to make the deduction that the early stages of the development of the organism are autonomous. The question lies not in autonomy, but in two basic common processes:

a) The subordinate significance of early stages of development in relation to the later ones, which have an adaptive significance.

b) The impossibility, at least in the enormous majority of cases, of preserving direct, morphogenetic ties with the environment. These ties are preserved in seasonal phenomena, for example, in cases of acceleration of processes of ovo- and spermatogenesis under the influence of temperature and light in bird.

6. The instability of morphogenital ties with the environment indicates how plastic the life processes of an organism are--under those conditions of existence in which any tie would serve as a brake on the processes of development.

7. Ties with the environment are more easily observed in those organogenesis, which are new for the given group and, in addition, they must be observed in such species as have most fully preserved primary relations with the environment (the differentiation of the lung in the tailed amphibian with the participation of oxygen, according to the experiments of A. A. Mashkovtsev).

8. In the majority of cases, the primary sources of morphogenital influence of environment are replaced by secondary sources, belonging to the organism itself. It is precisely this widely-diffused process of the replacement of the sources of morphogenesis which creates the seeming autonomy of ontogenetic morphogenesis in early stages of development, about which Roux speaks in a mistaken fashion, and after him, A. A. Mashkovtsev.

9. In a number of cases, it can be shown that the early stages have an indirect link with the environment, through correlative ties with later stages of development, with organs, possessing adaptive significance. The influence of changes in provisional organs can be noted, which possess an adaptive significance, on the processes of development of definitive organs.

10. A curious example of the influence of a change in the early stages of development upon later ones (the reconstruction of the processes of segmentation as a distant prerequisite for the formation of a powerful allantoid placenta) represents the processes of embryogenesis in placental mammals. In this case, correlative correlations have a character of graduated correlations, in which each preceding link is the indispensable prerequisite for the next one.

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